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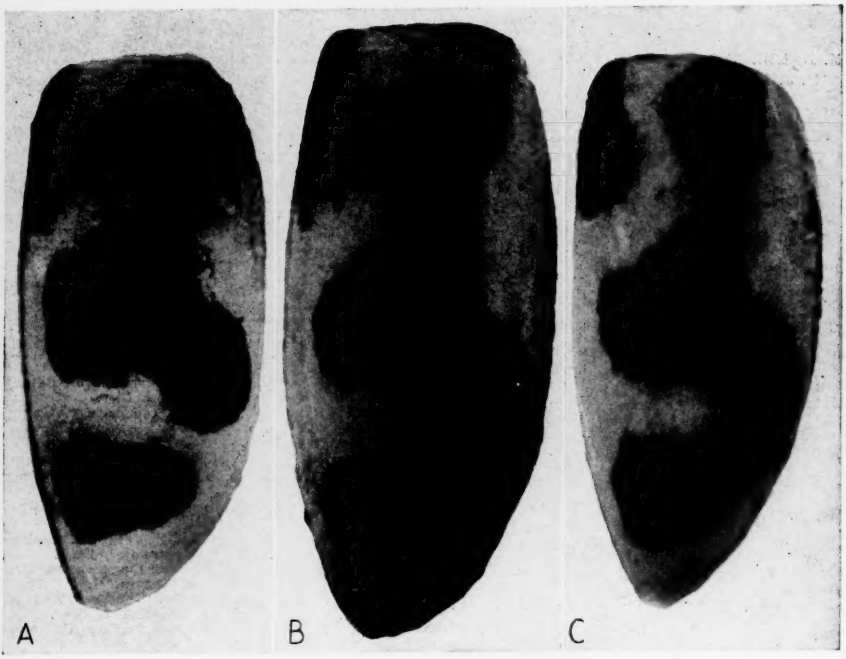

LADY BEETLE WING-COVERS
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History of Aberdeen-Angus Cattle

Varied Defects of Hands and Feet

Heredity and Length of Gestation

Defects in Purebred Swine

Chemistry and Embryology

VOLUME 34 NOVEMBER, 1943 NUMBER 11

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The

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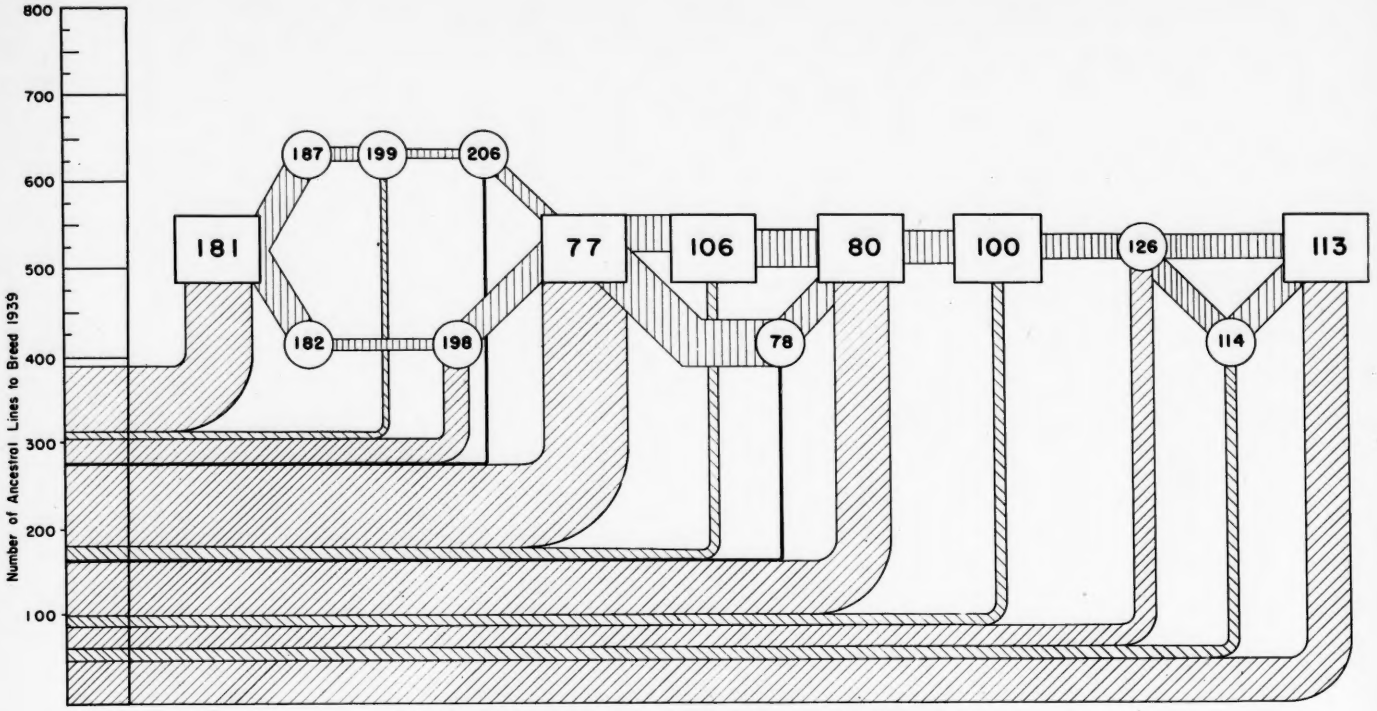

ANCESTORS OF THE ABERDEEN-ANGUS BREED

Figure 1

Analysis of the pedigrees of a random sample of the Aberdeen-Angus breed in 1939, shows that six sires (squares) and eight dams (circle) contributed just about half the ancestry. Sire 77 (Black Prince of Tillefour) has a relationship to the whole breed of 24.1 per cent, which means in terms of gene-constitution that he is virtually the grandsire of the entire breed. The smaller contributions of the foundation dams suggests that the Aberdeen-Angus breeders' concept of "families" overemphasizes the importance of the female line. See page 327 for details.

THE BREEDING STRUCTURE OF THE ABERDEEN-ANGUS BREED*

H. H. STONAKER*
Iowa State College†

THE object of the present study was to find how the breeding structure of the Aberdeen-Angus breed of cattle in the United States differed from random mating and to determine the causes for any departures found. The Wright and McPhee method[5] of sampling was used. This method has been applied in several breed studies. These were reviewed recently by Carter.[1]

Historical Background of the Breed

The Aberdeen-Angus breed originated as a cross between two somewhat similar strains of cattle indigenous to the Scottish counties of Aberdeenshire and Forfarshire. Forfarshire was formerly called Angus-shire. From the historical evidence available, the incidence of polledness and of black color was already high in these native stocks. The agricultural value of these cattle to Scottish farmers lay principally in their use for work stock and the production of feeders to be sold for fattening in the southern counties. Later with the development of turnip raising, the cattle were fattened in the northern counties and sold on the English market. This practice resulted in an increased interest in improving the cattle so that they would be more profitable under these conditions. The introduction of improved Shorthorn bulls for crossing on the native stock became a popular practice, and it seemed for a while that the pure native stock would become extinct. A few breeders, however, gathered together stocks of the native strains of the Aberdeen and Angus cattle and maintained their purity. The first published herd-book appeared in 1862 and a breed society was organized in 1879. Aberdeen-Angus were first imported into the United States in 1873. There were 38,737 purebred Angus registered during 1941.

Data Studied

Five samples, each consisting of 400 pedigrees of Angus cattle, were studied. These samples came from volumes 11, 20, 32, 39, and 46 of the American Aberdeen-Angus Herdbooks and included only animals born in the United States in the years 1900, 1910, 1920, 1930, and 1939. Regularly spaced pages in the herdbook were chosen and then from each page the first pedigree of an animal of the sex wanted and born in the right year was chosen for study. Equal numbers of males and females were included in each sample. A random line from the sire and another from the dam in each pedigree were traced to the earliest animals for which birth dates were recorded. These are hereafter called the "foundation animals." The average birth date of these foundation animals was 1850. With the generation intervals averaging 5.4 years (Table I), 1850 and 1939 were about 17 generations apart. One hundred thirty-six show winners, consisting of the first five animals in each class at the Chicago International during 1932 and 1941, were also analyzed.

Inbreeding and Inter-Se Relationship

The inbreeding and inter-se relationship percentages are shown in Table I. The inbreeding is equivalent to about one generation of half brother-sister mating. It is slightly higher in the Angus breed than has been found in any other breed of livestock yet studied except the Shorthorns. This may be due in part

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to the fact that the base period is earlier than in some of the other breeds. If the base year had been 1860 instead of about 1850, the inbreeding would have been 9.8 percent rather than 14.2 percent in 1930. This 9.8 percent can be compared with the 8.1 percent in the Herefords in 1930, relative to their ancestors in 1860.

From 1900 to 1939 the Angus inbreeding has tended to increase slightly, the fitted straight-line trend being $+.06\% \pm .06\%$ per year or about .3 percent per generation. This rate of increase in inbreeding during the last forty years is evidently less than it was at some earlier time in the history of the breed; otherwise the total inbreeding of the breed today could not be as large as it actually is. The ancestors responsible for the inbreeding (those found in both the random lines traced from the same pedigree) were not distributed uniformly throughout the different generations in the pedigrees, nor were their births uniformly distributed through the years. Instead a disproportionately large number of those common ancestors lived during the foundation period. Fifty-six percent of the inbreeding was toward common ancestors which were born before 1865. There were few ties in recent generations. Perhaps this indicates some difference between former and present breeding practices. It could, however, be due at least partly to two other circumstances. In the early period prominent animals could more easily spread their genes through the breed, since the breed at that time was much smaller in numbers and was centralized in Scotland. It may be necessary for some time to elapse before any animal's descendants can have been used so widely that large numbers of animals trace to it through both sides of their pedigrees. For example, 26 years elapsed between the birth of Earl Marshall, the breed's most prominent sire in recent years, and the time when he contributed much to the inbreeding of the breed.

In the 1932 show winners the inbreeding was 12.9 percent, which was slightly lower than in the whole breed, but the inbreeding of the 1941 show winners was 19.2 percent which was significantly higher than the sample of the whole breed.

The expected inbreeding if mating were entirely at random with respect to relationship would be $\frac{R}{2\text{-}R}$ where R is the inter-se relationship. The inbreeding expected was only about 62 percent of that actually found. This ratio was almost the same in each of the five periods studied. The excess of actual over expected inbreeding indicates that the breed has been separated slightly into partially isolated breeding groups.

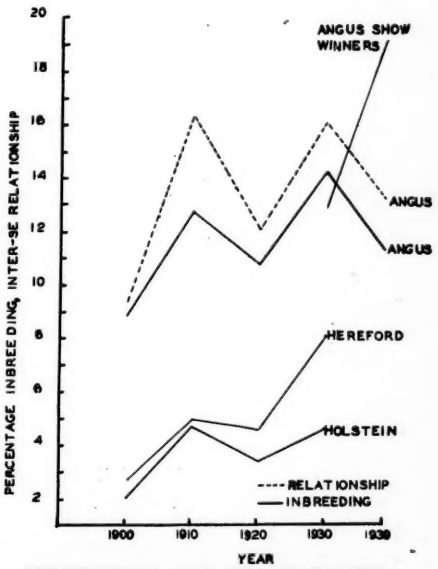
Amount of Inbreeding Due to a Finite Size of Population

Merely limiting the size of a population, as is done by pure breeding which prevents the introduction of outside blood, would by itself cause some inbreeding. It is pertinent to inquire whether the inbreeding found can be explained satisfactorily by this circumstance alone. Wright[3] has shown that in a population in which there are far fewer breeding males than females and in which all of the sires have equal chances to leave offspring the inbreeding will rise at such a rate that about $\frac{1}{8M}$ of the remaining heterozygosis is lost per generation where M is the number of males attaining breeding age.

A rough estimate of the number of sires being used in the Angus breed was made by assuming that the number of sires equals the number of breeders. The average number of breeders registering animals in each of the chosen years was 2,327; hence the number of sires is estimated to be 2,327. This yields only .005 percent of inbreeding per generation as the increase in the inbreeding which would result solely because outside blood cannot be introduced into a pure breed. Pure-breeding by itself in a population as large as the Aberdeen-Angus breed can not be considered as responsible for more than a very small fraction of the average rate of increase in inbreeding actually found. Two conditions in Wright's formula may fail to be met here. One is that mating may

not be random. The inter-se relationship indicates that it was not quite random. This will account for a little of the discrepancy. The other condition is that the males entering the breeding herd have equal chances to leave offspring. If this were so, the actual numbers of offspring of each sire should vary in a Poisson distribution. Actually it seems probable that the variation in the number of offspring per sire (considering only those which enter purebred breeding herds, since they alone have a chance to contribute to the future inheritance of the breed) is far larger than in a Poisson distribution. Consequently, as Wright emphasizes, the *effective M* of the formula is far smaller than the *census M*.

Distance may of itself keep mating from being entirely random within the breed. It thus may raise the inbreeding and lead to some partial isolation, even when no absolute barriers to exchange of breeding stock exist within the breed. The greater the distance which animals travel before they meet their mates, the more unlikely it is that they will mate with relatives. Conversely, if animals tend to mate with those bred in the same vicinity, generation after generation, then the average relationship between mates and the resultant inbreeding are increased. There is some tendency for Angus breeders to use sires bred near their own localities. A sample of 100 breeders in 1930 traveled an average of 361 miles for their sires. Within the area circumscribed by that distance there were on the average about 339 breeders. In 1939, another sample of 100 breeders went 352 miles for their sires. By then the number of herds had nearly doubled and the average breeder had access to 658 breeders within a radius of 352 miles. If the effective number of sires in an area were equal to the number of breeders, the isolation expected from distance would account for an increase in inbreeding of .04% per generation in 1930 and .02% in 1939. This is only about ten percent of the actual .3 percent increase in homozygosis per generation. Apparently geographic distance



INBREEDING AND RELATIONSHIP
Figure 2

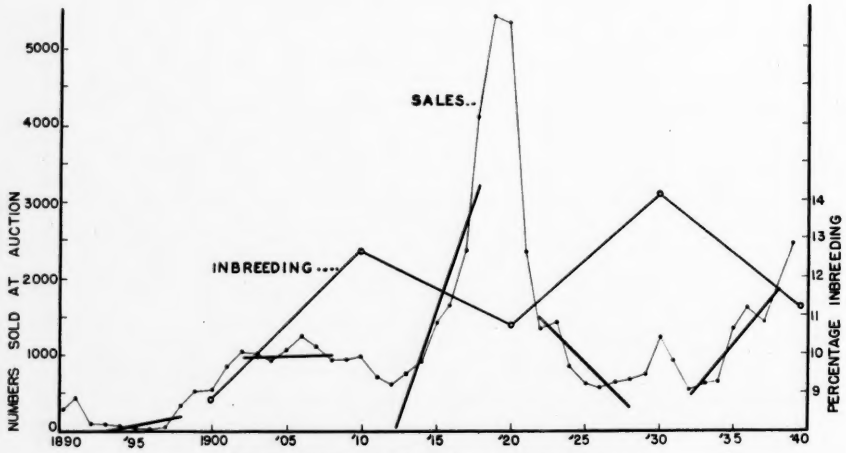
The inbreeding and relationship of the Aberdeen-Angus breed as a whole is compared with the Hereford and Holstein breeds. The Angus show-winners group showed a marked increase in inbreeding in 1939.

is only a minor cause of the partial subdivision of the breed which keeps the inbreeding higher than that expected under random mating.

Short Time Fluctuations in the Amount of Inbreeding

Figure 2 shows some large fluctuations in the inbreeding percentages for the five different years. These fluctuations deviate significantly from the regression line, but the causes of them are not entirely clear. An indication that they are due to something not confined to one breed is the fact that other breeds which have been studied recently show tendencies to vary in the same direction at about the same time. It is plausible to suppose that these fluctuations result from the way economic depressions and booms affect the breeders' mating systems and cause large fluctuations in the numbers and size of purebred herds.

Breeders would more often use sires



INBREEDING AND SALES COMPARED
Figure 3

The relationship between breeder's practices and the economic cycle of periodic booms and depressions is illustrated here. Periods of decreasing sales tend to be times when inbreeding increases and vice versa. The short lines are sales trends for seven-year periods ending two years before the sample was born. See text below.

and dams which they have bred themselves when there is little opportunity to sell surplus breeding stock at a profit. On the other hand, when prices are good and purebred cattle are selling rapidly there may well be a greater tendency for breeders to go outside of their own herds and communities and to spend more money for new blood from other herds. As a test of this, Figure 3 shows the numbers of purebred Angus sold at auction and the subsequent inbreeding found in samples of the breed. The short lines are trends during the seven-year periods ending two years before each sample was born. In general, periods of increasing sales were followed by low inbreeding and periods of decreasing sales were followed by high inbreeding.

Also the percentage of matings in which both the sire and dam were bred by the same breeders may be an indicator of the extent to which the exchange of breeding stock had become highly local. The breeders of the sires and dams were tabulated for five samples of 200 pedigrees each, which were selected at random from animals born in each of the years 1900, 1910, 1920, 1930, and 1939. For the five samples the percentage of cases in which sire and dam were bred by the same breeder were 9.0, 6.5, 7.5, 17.5, and 14.0, respectively. The changes in these percentages parallel the changes in inbreeding closely in the last two intervals but not in the first two.

Although more of the sires and dams are bred in the same herds when the inbreeding is highest, the inter-se relationship fluctuates with the inbreeding rather than in an opposite direction as would be expected if the fluctuations in inbreeding were due mainly to individual breeders starting or ceasing to breed within their herds more than usual.

It may be that there are breeders who maintain nuclei of registered breeding stock but sell registered offspring only when the value of registered animals is relatively high. The periodic entrance into the herdbook of more animals from such herds might be the cause of the decrease in average relationship during boom times.

Prominent Animals in the Breed

Approximately fifty percent of the random ancestral lines in 1939 traced to

one or more of the six animals in the upper lines of Table I. Figure 1 shows this graphically. Several of these animals were closely related to each other and thus they accumulated large amounts of collateral relationship to the breed. The widths of the paths in Figure 1 vary with the number of lines tracing through each. For example, Hanton, 80, was found in 40 lines tracing to him through 106, in 37 lines tracing to him through 78, and in 66 lines through others of his descendants than those shown. Hanton's collateral relationship to the breed comes through the lines tracing to his ancestors through other relatives such as cousins. Each 100 paths represents approximately 12.5 percent relationship to the breed.

Earl Marshall, 183780, is the only recent example of an animal highly related to the breed through his direct descendants. About two-thirds of his relationship to the breed is direct from his many sons and daughters, the other third being collateral through his sibs, cousins, etc. Blackcap Revolution, 287269, was a son of Earl Marshall and is highly related to the breed largely because of the cumulative importance of Earl Marshall's other offspring. Only 43 percent of Blackcap Revolution's total relationship to the breed is direct through his own sons and daughters; the rest resulted from the influence of sons and daughters of his ancestors other than the ones through which he descended.

Herds in Which the Foundation Animals Were Bred

Five herds provided about 65 percent of all foundation stock and were thus the important fountainheads of the breed. About one-fourth of all lines come from animals bred in the herd of Hugh Watson. This verifies the prominent place his herd is given in most of the breed histories. This picture of the importance of herds concerns only the foundation animals of the period when birth dates first began to be recorded. Breeders who began their work later with animals purchased from the earlier herds would not appear in a tabulation like this, although their achievements and influence on the breed might even have been greater than those of Hugh Watson whose farming operations extended from 1818 to 1860.

Discussion

The comparatively small amount of inbreeding which has resulted from pure breeding for so long a time indicates that the genetic diversity within the breed today is but little less than it was among the foundation animals. It seems likely that large amounts of improvement in beef qualities are still possible without requiring such extreme measures as the introduction of new blood from other breeds to increase genetic diversity and opportunity for selection.

Increases in homozygosis seem to have been largely the result of two things: first, the tendency for breeders to linebreed to certain animals, a tendency which in the early years may have been greatly facilitated by the relatively small number of herds centralized in Scotland; second, distance between herds has partially prevented complete random mating in the breed.

Short time fluctuations in inbreeding are similar in the Angus, Hereford, and Holstein breeds. It is suggested that these shifts reflect the effect of economic conditions on the population's breeding

TABLE I. Inbreeding, Inter-Se Relationship and Length of Generation.

Year	Actual Inbreeding	Inter-Se Relationship	Average Generation Interval in years
1900	0.9 ± .9%	9.4%	4.9
1910	12.7 ± 1.1	16.3	5.03
1920	10.8 ± 1.0	12.2	5.13
1930	14.2 ± 1.2	16.1	5.23
1939	11.3 ± 1.1	13.3	5.43

TABLE II. Animals most highly related to the breed.

Animal	Reg. No.	Percentage Relationship to Breed				
		1900	1910	1920	1930	1939
Black Prince of Tillyfour	77	24.1	29.1	25.9	26.8	24.1
Hanton	80	21.5	22.3	18.9	23.4	21.3
Young Viscount	181	18.3	20.6	20.4	22.0	17.5
Rob Roy MacGregor	106	18.2	20.0	19.1	23.1	14.9
Grey Breasted Jock	113	18.1	26.6	15.1	16.6	10.5
Pat	100	19.5	18.3	13.2	17.2	10.8
Earl Marshall	183780	-	-	2.9	9.8	14.0
Blackcap Revolution	287269	-	-	-	8.7	12.0

structure. As yet, the causes of these shifts are not fully understood.

Only nine of the 26 animals having over five percent direct relationship to the breed were cows, and none of these cows was among the breed's eight most important animals. This suggests that the foundresses of the lines of descent traced only through the female line (called "families") actually have not contributed enough to the breed genetically to justify as much emphasis as is the custom of Angus breeders to place on family names.

The relative importance of the various early sires had not previously been measured objectively except by Malin.[2] He found that on a "percentage of blood" basis the genetic constitution of twenty of the breed's most prominent sires of winners in 1918-22 was 7.6 Cupbearer, 15.0 Black Prince of Tillyfour, 6.7 Trojan, 10.2 Young Viscount, and 6.8 Juryman. On a comparable basis the figures found in the 1920 breed sample of this study were 7.5, 14.3, 6.3, 9.6, and 4.7. Early breed histories emphasized the importance of nearly all of the eight bulls found most frequently in both this and Malin's study.

Summary

The average inbreeding percentages of samples of the Aberdeen-Angus breed of cattle born in the United States in 1900, 1910, 1920, 1930, and 1939 were 8.9, 12.7, 10.8, 14.2, and 11.3. Inter-se relationships in each of the five samples are 9.4, 16.3, 12.2, 6.1, and 13.3 percent. The inbreeding expected from the inter-se relationship is only about 62 per cent of that actually found. Thus there is some slight tendency for mates to be more closely related to each other than if mating were absolutely random with respect to pedigree. About ten percent of the average .3 percent rise in inbreeding per generation appears to be the result of partial isolation between herds on account of distance.

Fluctuations in inbreeding from sample to sample are significant and parallel the fluctuations in inter-se relationship.

Black Prince of Tillyfour (77) is 24.1 percent related to the breed. This is practically equivalent to his having been a grandsire of the whole breed. Relationships of other important animals are Hanton (80), 21.3; Rob Roy MacGregor (106), 14.9; Grey Breasted Jock (113), 15.5; Earl Marshall (183780), 14.0; and Blackcap Revolution (2872-69), 12.0 percent.

Over 60 percent of the genes in the breed probably came through foundation animals bred in only five herds. Of these, the Hugh Watson herd was the most important.

The average interval between generations was nearly 5.4 years.

Except in a few details, the breeding systems used in the Aberdeen-Angus breed in the United States appear to be much like those in other breeds of cattle.

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INHERITANCE IN LADY BEETLES

I. The spotless and spotted elytra of *Hippodamia sinuata**

A. FRANKLIN SHULL

THE great variability of the patterns of lady-beetle species has attracted the attention of naturalists for many decades, and invited speculation concerning its significance in evolution. Evidence of genetic segregation was observed at least as early as the closing years of the last century, but not always so interpreted. The black variety of *Adalia bipunctata,* sometimes labeled a species of *Coccinella* in the early collections, was crossed by Burgess[1] with the normal red form, and both types appeared in the progeny. Although the female might not have been virgin in this first cross, the fact that the male possessed the rarer character and that this character was borne by some of the offspring indicated that he was the real father. Later matings using females known to be virgin confirmed the segregation. Burgess debated whether the black form might be a different species, and seemed to expect that if it were, the hybrid would have been intermediate; but today his results would be taken to mean that the red and black differed in one gene.

Later experimenters expected segregation, but in fitting their results to ordinary Mendelian rules were handicapped by difficulty of assuring virginity of the females. Most of the early supposedly hybrid progenies were obtained from pairs taken *in coitu* in nature, and under these circumstances the female might have mated earlier. Schröder,[29] recognizing this source of confusion in his crosses of *Adalia,* sought later[30] to remove it by using beetles just emerging from hibernation. After this precaution he got only one kind of offspring from each first cross; but even if spermatozoa could not survive over winter in the female, he could have got this expected result only if the phenotypically dominant parent were homozygous. The experiments of Johnson[16,17] on various species, and of Hawkes[8] on *Adalia* and[9] on *Coccinella* were often started with females not assuredly virgin, and some of the results were held to show they were not virgin—though heterozygosis might be the explanation of some such results. Forms regarded as belonging to different genera were taken in copulation by Marriner,[20,21] with progeny indicating segregation and some degree of dominance, though the interpretation was doubtful. The hybrid announced in the first of Marriner's papers was held by Capra[2] not to be a hybrid, merely the variety *10-pustulata* of *Adalia* (*Coccinella*) *10-punctata,* but the second publication was based partly on a known hybrid.

No hesitation in assigning Mendelian explanations to results of crosses was felt by Palmer.[24,25] She was able to cross, without difficulty, five forms regarded by many as distinct species of *Adalia.* Though no system of genes was proposed, she found segregation and varying degrees of dominance. Zimmermann[44] also arrived at simple Mendelian results in crosses between two varieties of *Epilachna chrysomelina,* in which light pronotum proved to be dominant over dark, and merged ocelli nearly dominant over separate.

Multiple Alleles

Some confusion in the early interpretations resulted from overlooking multiple alleles. In *Coelophora inaequalis* Timberlake[34] concluded that inheritance was segregative, but in some measure non-Mendelian because unexpected offspring appeared. His results were entirely regular, however, on the assumption of multiple alleles, as Dobzhansky[6] pointed out. The order of dominance in the triple series he studied is nine-spotted >normal >black. Tan and Li[33] proposed three pairs of genes to explain the patterns of *Harmonia axyridis,* but Hosino[12] concluded that the contrasted patterns are really multiple alleles. Tan

*Contribution from the Department of Zoology, University of Michigan.

and Li presented several results not in harmony with the multiple-allele explanation, but these Hosino[14] regarded as the results of experimental error—which can easily happen in work with these beetles. Hosino[13 14.15] added other alleles to this series, which now includes eight patterns. Between these alleles dominance is sometimes complete, sometimes partial or lacking.

Palmer's results[24.25] are also explainable on the basis of a series of multiple alleles, which may have been her concept of their relations to one another though she does not specifically so state. The order of dominance (probably not always complete) in *Adalia,* as she found it, was apparently *melanopleura* >*bipunctata* >*annectans* >*coloradensis* >*humeralis*. There seems to be no specific reason in her work for putting *melanopleura* above *bipunctata* in this order, though she apparently assumes (Palmer,[25] p. 299) that that is its position. Support for the conclusion that these forms are multiple alleles is presumably afforded by the work of Lus[19] on the same species, *Adalia bipunctata.* Lus concluded that eight forms of this species are dependent on genes at the same locus, though the evidence is regarded by Timoféeff-Ressovsky[36] as not quite conclusive. The names given these forms are all different from those given to Palmer's "species," and from the illustrations presented most of them are phenotypically different from hers. With respect to two of them, however, there is no clear difference. Probably the form called by Palmer simply *bipunctata* (two black discal spots on a red ground on the elytra, and a black M on the pronotum) is the same as *forma typica* (gene S^t) of Lus; and Palmer's *humeralis* (red discal spots and red shoulder patches on black ground on the elytra, and a mostly black pronotum) could be identical with *4-maculata* (S^m) of Lus. If either of these suggested identities is real (and possibly even if they are not), the two series of alleles become a single one. If they do, however, the order of dominance is confused (perhaps by dominance-modifying genes); for *humeralis* is most recessive in the American alleles, *4-maculata* second most dominant in the Russian; and *bipunctata* is near the top of the dominance order in America, while *typica* is fifth in order in Russia. It would be interesting to know whether this large series may not also extend to another species, *A. decempunctata,* in which Lus discovered three alleles of a series. Among these three, the one at the bottom of the dominance order (*bi[illegible]lata*) is phenotypically very simila[illegible]he one (*sublunata*) at the top of the [illegible]minance order in *A. bipunctata.* One could speculate on the existence of a series of mutations of the same gene, spread through the two species, but divided into two groups by interspecific sterility. Lus does not indicate whether any species crosses were attempted.

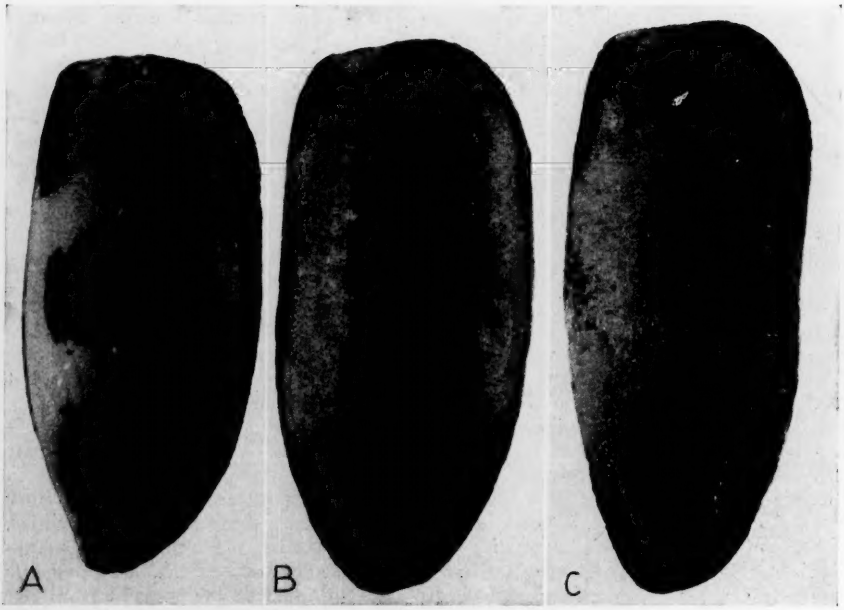
Species crosses, it will be observed, are readily effected, though views of what constitutes a species (heretofore very discordant) may be profoundly influenced by the genetic work as the latter accumulates. Johnson[17] reported species crosses which were probably correctly so judged, since Johnson's tendency, according to Dobzhansky,[6] was to assemble species rather than split them. Even a generic cross (between *Adalia bipunctata* and *Coccinella variabilis,* see *ante*) was reported by Marriner[20] both as effected in the laboratory and as discovered in nature; and this hybrid was sufficiently fertile to be bred into later generations. The same author[21] suggests further that hybrids between *Adalia* and *Mysia* are found in England.

Indications of inheritance too vague to lead to any explanation were observed in *Harmonia axyridis* by Dobzhansky[4] before the conclusive genetic work of Tan and Li, and of Hosino. His discovery that each of several fluctuating (and overlapping) types had a different reaction norm suggested that these types had a genetic basis, and may well have been influential in bringing about the later experimental work. Correlations between different parts of the pattern could be interpreted on at least a physiological basis, perhaps a genetic one. Dobzhansky[4] established a correlation

between pronotum and elytra in *Harmonia axyridis,* Schilder[27] between the parts of the elytral pattern in *Adonia variegata,* and Zarapkin[40] between the position of spots and their size and tendency to merge in *Propylaea 14-punctata.* These correlations, if not of genetic significance, must bear on questions of physiology of development, a field directly explored by Zarapkin[39] in *Coccinella 10-punctata* with respect to origin of pigment (which he regarded as being subject to a directed variability) and to formation of pattern. The fact that different races of *Epilachna* respond differently to temperature in the extent of their black spots (Timoféeff-Ressovsky[35]) presumably means that there is a genetic basis for this response. A number of other studies merely or chiefly described variability—for example, that of Reichert[26] for *Adalia bipunctata;* of Hosino[11] for *Harmonia axyridis;* of Meissner[22] for *Propylaea* and *Coccinella* with respect to the tendencies toward lightness and darkness; of Schilder[28] for *Propylaea* from which one could almost infer—as the author does not—dominance of reduced spotting over increased spotting; of Vogt and Zarapkin[38] for *Coccinella decempunctata* arriving at a statistical rule for the frequencies of patterns and at the conclusion that variation is directed; of Zarapkin[42,43] on the relation between the frequency of spots and the time of their ontogenetic appearance, leading again to the concept of directed variability; of Schilder (in part, see *ante*) on *Adonia variegata;* and of Smirnov[31] and Timoféeff-Ressovsky and Zarapkin[37] in which lady beetles furnish part of the illustrative material for more or less purely mathematical considerations. While the phenomena described in these papers doubtless have a genetic basis in part, the authors are concerned with genetics only in a minor way or not at all. They may, however, have helped stimulate the directly genetic experiments.

One of the early uses of genetic knowledge of these beetles to the furtherance of biological theory will be (and has been) in relation to population statistics and geographic variation, and through these to the evolution of the coccinellid family. Dobzhansky[4] and Tan and Li[32] gave the proportions of the various types of *Harmonia axyridis* in different populations, while the frequency of omission of spots in *Hippodamia convergens* was ascertained by Dobzhansky.[6] Marriner[20] reported the seasonal prevalence of the red and black forms of *Adalia bipunctata* in England, the former being more abundant in spring, the latter in late summer. Additional varieties of this same species have been studied by Timoféeff-Ressovsky[36] near Berlin not only with respect to their frequencies in the population, but as to changes in those frequencies during the summer and as to their survival values in hibernation. The changes indicate that selection favors the black variety in summer (in agreement with Marriner for England), the red variety in winter. An increase in the frequency of many-spotted individuals of *Adalia bipunctata* in a certain area in England from one year to the next seems to have been brought about by Hawkes[10] by the artificial introduction of the darker forms into it. The tendency of the spots in *Coccinella 14-punctata* to merge with spots in front of or behind them, or beside them, was determined by Moderegger[23] for different populations, but the difference was not proven significant.

The importance of such statistics of populations is considerably enhanced if they are found to have a relation to geography, with or without any relation to climate. The lead in such geographic studies was taken by Dobzhansky[3] who traced the variation of two species of *Adalia* from Europe to central Asia, where they overlapped somewhat in their phenotypes, and Dobzhansky and Sivertzev-Dobzhansky[7] who, for *Coccinella septempunctata,* demonstrated a center for small spots in south central Asia and in Persia, and an increase in the spots radially from this area toward the west and northwest, and especially toward the east and northeast. A similar study of *Hippodamia convergens* (Dobzhansky[6]) showed that reduction of spots is much more frequent in California than in the



LADY BEETLE WING-COVER PATTERNS
Figure 4

A—Right elytron of the lady beetle *Hippodamia sinuata* var. *spuria*. *B* and *C* are right elytra of the spotless variety of *H. sinuata*. Note the short stripe on the inner angle of *C*.

eastern United States. Comparable geographic differences were observed for several other species, and Dobzhansky suspects a general relation to humidity and perhaps temperature in most of them. Such varieties, whether geographic or not, Dobzhansky[5] holds to have a genetic origin, in that they are differentiated out of an antecedent mixed population. Landis and Mason[18] also refer to geographic differences in variation in *Epilachna varivestris*, pointing out that in Mexico the tendency is to omit spots, in Ohio to merge them. Population differences in *Epilachna* were discovered by Zarapkin[41] with respect to the distribution of pigment among the several spots, such that specimens could be correctly allotted to their areas on that basis.

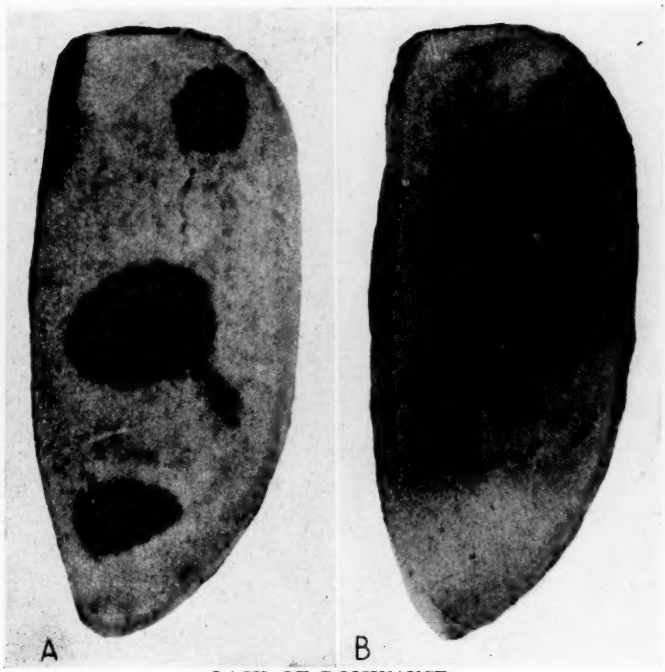
The literature of coccinellid genetics has been reviewed here in outline somewhat beyond the requirements of the new data to be presented in this paper, with the expectation that in any future publications in the same general field it will not be necessary to repeat the statement of fundamental relations.

Pattern of *Hippodamia sinuata*

Through the courtesy of Professor H. B. Yocom I received in the spring of 1942 from near Eugene, Oregon, a mass of hibernating beetles most of which were *Hippodamia sinuata* var. *spuria*.*

The pattern of this variety is shown in Figure 4*A*. In the majority of individuals the spots are separate, except that across the middle of the elytron is a bilobed spot which, from a comparison with other species of *Hippodamia*, may be regarded as a merger of two spots. In many beetles, however, the bilobed spot is connected to a variable extent with the spot behind or in front of it, or

*Professor Melville H. Hatch kindly identified the material.



LACK OF DOMINANCE
Figure 5

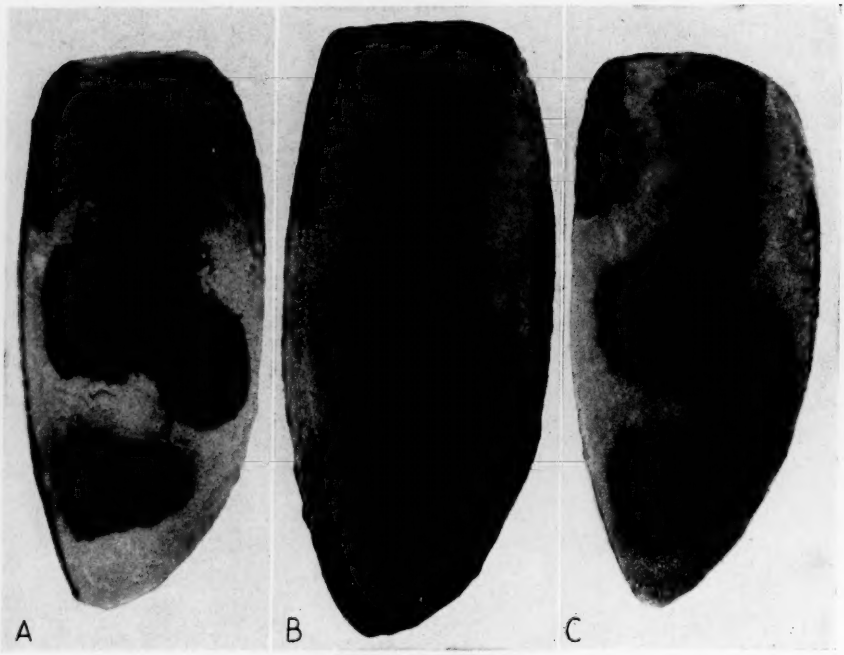
Right elytra of two heterozygotes showing the lack of dominance of spotless and spotted. Of 20 hybrids between the spotted and the spotless form, one had no spots and the 19 others had much reduced spots.

with both of these. In none of the beetles in this hibernating mass was the bilobed spot connected with the scutellar spot which is shared by the two elytra at their inner front corners, though occasionally an angle projecting anteromesially from the bilobed spot suggests an approach to such a connection. The ground color is approximately ochraceous buff (Ridgway, Color Standards and Nomenclature).*

Among the spotted beetles were a few which had no black markings except (usually) a short and slender dark scutellar stripe (Figure 4*B*, *C*). Their color was essentially the buff of the ground color of the spotted type. This form is here called "spotless."

Beetles of both the spotted and spotless kinds were bred, and from their descendents were selected virgin females of the spotted form and males of the spotless, which were crossed. Of the 20 offspring obtained, one was entirely spotless (except the scutellar stripe which hereafter will be ignored), and the other 19 had much reduced spots. The size of the spots in these 19 varied considerably, but never even closely approached those of the spotted pattern. Two grades of the intermediate pattern are presented in Figure 5. The one at the left is not quite the darkest; it shows a slight indication of the outer lobe of the bilobed spot. In one other individual this outer lobe was a mere cloud, but separate from the inner lobe. At the other extreme of

*One beetle in the entire group, discovered too late to do any genetic work with it, had its spots so enlarged that the whole elytron was solid black except a narrow streak of buff along part of the margin.



SPOTTING PATTERNS
Figure 6

Types of coalescence of spots on elytra of *H. sinuata* var. *spuria*. Note that the bilobed central spot can be united by a bridge either to the forward spot (*A*), to the rear spot (*B*), or to both (*C*).

this series the spots became mere hazy patches. When only one spot was present it was at midlength; when two were present, it was usually the anterior outer (humeral) spot which accompanied the middle one.

The spotless pattern is thus not quite dominant over the spotted. There was overlapping of the heterozygote with the spotless homozygote, but always (in these experiments) a sharp gap between the heterozygote and the spotted homozygote.* To make the presentation of all the crosses uniform, the above results are included in the first line of Table I, where all the other successful experiments are recorded. All beetles with reduced spots, even if these are mere clouds, are listed as intermediate. The one spotless one in the first line is of course heterozygous, like the intermediates.

One mating not included in the table, spotless × spotless, was attempted several times, but offspring were obtained in only one experiment. In this successful mating one parent had faint cloudy spots, and was used on the chance that it might be homozygous spotless because spotless beetles were scarce at the time. The offspring were, however, of two kinds, spotless and intermediate. They are accordingly included in the second line of the table as progeny of intermediate × spotless.

With the exception of the seven beetles marked with an asterisk, the results in the entire table are in harmony with the assumption that only one gene differentiates spotless from spotted, and that

*In the classification of the hibernating mass there were only three or four beetles which required a second observation to decide whether they were intermediate or spotted.

dominance of spotless is incomplete. One of these seven (in the first line of the table) is known to be heterozygous; it is therefore justifiable to conclude that the spotless ones of the third and fourth lines are also heterozygous. Attempts to breed them for a more direct test failed.

Variations of spotted pattern

The only author to report the breeding of *spuria* is Johnson,[16] who regarded it as a separate species. He bred 13 females, sometimes after mating with unknown males, and records the pattern of their offspring. No later generations were reared. All these beetles were of the spotted pattern and the variations he observed were mostly related to the separation or coalescence of the spots. No very definite conclusions could be reached. He states that the inheritance of the scutellar stripe is segregative, but apparently this merely meant that it could be present or absent. He recognized two centers of variation of the spotting, but not two unit characters. The form which Johnson called *sinuata* he did not breed at all.

Whether the coalescence of the spots of the spotted pattern has a genetic foundation was not specifically tested in my own experiments, but some results bear on that question. All parents have been preserved, except a few which escaped or died and could not be found. Unfortunately, as a labor-saving device, the matings were not always of single pairs. Several females of one kind were confined with several males of a contrasted kind. When offspring were obtained, they could be the progeny of any one or more of each of the sexes among the adults. With respect to the characters which were being directly studied, and so long as the heredity proved to be simple, this method was satisfactory; but for any character which differed in some minor respect among the females or among the males, the results would be questionable.

In four of the matings between spotted and spotted all females and males used had the bilobed spot separate from the others. Their offspring included some with coalesced spots, the details being given in the first line of Table II. In other experiments one or more of the adults had the bilobed spot connected with either the humeral or with the apical (most posterior) spot (Figure 6). In Table II the experiments are described according to the type of coalescence shown by the possible parents and the progeny are sorted with respect to their coalescence. There is little in this table to suggest that the merging of spots is hereditary. More coalescence occurred in progenies which certainly were derived from parents without coalescent spots than in progenies whose parents may have had coalescent spots. It seems more likely that merging is dependent on developmental or possibly environmental fluctuations.

Frequency of the pattern genes

In their bearing on evolution, the importance of alternative genes depends on their abundance. While no comparison of the frequencies in different populations of the genes here studied can be made at once, the facts for this one population should be put on record. The beetles sent from Oregon were in a hibernating mass of over 23,000 individuals. It is found to consist of 20,974 spotted, 2,125 intermediate, and 143 spotless ones. The first of these numbers is fairly accurate, since there is little or no overlapping of the phenotypes of spotted and intermediate beetles. The other two numbers are doubtful because heterozygotes may have only the faintest indications of spots or be entirely spotless.

On the basis of these numbers it may be computed that 5.00% of the genes are *S* (spotless) and 95.00% *s* (spotted). It would be expected therefore that the spotted beetles (*ss*) would constitute 90.24% of the population, the intermediates (i.e., heterozygotes, *Ss*) 9.51%, and the spotless (*SS*) 0.25%. Thus the phenotypically spotless individuals, which constitute 0.62% of the total, are 2.46 times as abundant as the genotype *SS* should be. Only 40.7% of the pheno-

typically spotless beetles (about 58 of the 143) may be presumed to be genotypically *SS*. The other 85 spotless should be heterozygotes in which *S* is completely dominant. That is, in about 3.85% of the heterozygotes, spotless is completely dominant; in the rest the spotted gene comes to expression in some degree. These computations rest on the assumption of random mating and equal fertility and viability of all three types.

If the discrepancy between spotless pattern and the *SS* genotype represents merely the overlap of *Ss* and *SS*, the proportion of heterozygotes which were spotless was less in the natural population (3.85%) than in the experiments (15.22%). Another explanation of the discrepancy could be selective mating favoring that of spotless with spotless, though in the experiments such matings failed. The larger number of spotless can hardly be caused by differential mortality, for in the experiments the spotless beetles appeared to be the least vigorous. This appearance of lower vigor seems to be confirmed by the smaller number of spotless individuals among the progeny of intermediate × intermediate, in line 5 of Table I.

TABLE I. Results of crosses involving the spotted and spotless patterns of Hippodamia sinuata.

Parents		Offspring		
Female	Male	Spotted	Intermediate	Spotless
Spotted	Spotless	0	19	1 *
Intermediate	Spotless	0	11	12
Intermediate	Spotted	4	4	1 *
Spotted	Intermediate	24	16	5 *
Intermediate	Intermediate	50	114	41
Spotted †	Spotted	306	0	0

* These spotless beetles are interpreted as heterozygotes in which spotless is wholly dominant.

† Among these matings were some which used spotted beetles derived from intermediate parents, and which therefore could have borne the spotless gene had spotted been dominant.

TABLE II. Showing probable lack of inheritance of coalescence of spots in Hippodamia sinuata.

Possible Parents	Offspring			
	Bilobed spot distinct	Bilobed joined with humeral	Bilobed joined with apical	Bilobed joined with humeral and apical
Bilobed spot distinct	103	12	2	3
Bilobed joined with humeral in 1 of 11 parents	168	6	1	0
Bilobed joined with apical in 2 of 5 parents	9	0	2	0

Summary

The spotless pattern of *Hippodamia sinuata* differs from the spotted (variety *spuria*) in just one gene. The spotless type is not quite dominant; though a few of the heterozygotes are strictly spotless, most of them have reduced spotting. There is little or no overlapping of the phenotype of the heterozygote and that of the spotted homozygote. In an Oregon population, the spotless gene was present in 5% of the pertinent chromosomes, the spotted gene in 95%. Only about 41% of the phenotypically spotless beetles are homozygous for the spotless gene. The occasional fusion of spots, other than the pair in the middle of each elytron, in the spotted pattern has no clear genetic basis.

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THE SCULPTURING OF GROWTH

ALTHOUGH not published as a continuation of the author's well known *Chemical Embryology,* the present work* closely resembles it in format and method of approach. As in *Chemical Embryology,* the attack is on a large scale over a wide front, with the difference that in this book the main effort is concentrated on the organizer problem. *Biochemistry and Morphogenesis* is divided into three parts respectively titled: The Morphogenetic Substratum, The Morphogenetic Stimuli, and The Morphogenetic Mechanisms. Part I, consisting of 93 pages, summarizes recent literature dealing with the chemical composition of the egg and with problems of embryonic nutrition. It brings up to date the corresponding chapters of *Chemical Embryology.* Part II, 405 pages, presents an exhaustive summary of published experiments bearing on the physiology of determination in vertebrates and invertebrates. Part III, of 172 pages, covers recent work on the special metabolism of the embryo. There follows a glossary of special terms and an astonishing bibliography of approximately 5,000 references, listing apparently every publication of any importance which has appeared in this field in the last ten years. The volume is fully indexed. Possibly as a compromise with paper-rationing, the author has adopted an unfortunate shorthand for indicating chemical structures; otherwise there are but few signs of war in the make-up of this book. It is noteworthy indeed that a scientific treatise of such size and elaborateness has been published in England at this time.

The Evocator Mystery

The most important section is Part II which occupies over half the book, and deals with the complicated field of organizer phenomena wherein embryologists caught the first exciting glimpses of a possible causal connection between

**Biochemistry and Morphogenesis,* by Joseph Needham; xvi + 787; 328 figs.; $12.50; Macmillan, 1942.*

chemical process and morphological structure. The discovery by Spemann in 1931 that the implantation of non-living material into an embryo can lead to the formation of secondary structures should, by all precedents, have been the first step leading to the isolation and chemical identification of the agents involved. The way seemed open to an understanding of the biochemistry of morphogenesis. Unfortunately, this has not been the case. The intense exploitation of this field during the past decade has uncovered unsuspected difficulties; complication has followed complication until the original, clear-cut, all-or-none organizer effect has been all but lost in the traffic. To quote Needham: "Although much has been achieved . . . we have come to see that the problems are often far more complex than had first been thought, and that after all the larger part of the mystery remains in that we can as yet form little idea of what constitutes reactivity—the competence to react to the morphogenetic inductor."

The marshalling of the facts which have compelled this conclusion is part of the task of this section of the book. Beginning with a general discussion of embryonic determination, the author proceeds to a consideration of amphibian morphogenesis. The mapping of presumptive regions and the fundamental experiments on the primary organizer are described. Investigations of the chemistry and metabolism of the organizer region, in which Needham and his collaborators have taken a leading part, are presented in detail. An interesting, if inconclusive, discussion of organizers and cancer follows. The chapter on amphibian development concludes with a discussion of regional differentiation of the embryo and the functioning of secondary organizers. The remainder of Part II includes chapters on organizer phenomena in vertebrates other than amphibia, on determination in insects, and on determination in echinoderms. A valuable chapter on genes and organizer phenomena summarizes embryological and genetical experiments on the role of the nucleus in development. Needless to say, the relation to biochemistry of much of the work discussed here is exceedingly tenuous, just as the chapters in Parts I and III dealing mainly with chemistry contain but few morphogenetic implications.

As has already been indicated, the main emphasis in organizer studies has passed from the evocator substance to the tissues which react to it. Nevertheless, much interest still attaches to the chemical nature of the substance (or substances) in dead tissues which, when placed in contact with living embryonic tissues, can cause them to differentiate. What appears to be a straightforward problem in preparative chemistry turns out to be complicated by the fact that the reacting tissue also contains the evocator, but in a masked form. The chief difficulty lies in determining whether a given substance is intrinsically active, or whether it merely unmasks active material. The problem is not simplified by the fact that a wide variety of pure chemical substances is capable of calling forth inductions of neural tissue. In discussing this work, Needham summarizes the evidence for his own (tentative) conclusion that the evocator is steroid in nature. The two main arguments brought in support of the view that synthetic hydrocarbons act directly to produce inductions are, first, that they are active at lower concentrations than any other substances known to give the effect and, second, that the inductive action of at least one hydrocarbon shows an optimum dosage, above and below which the number of inductions falls off to zero. Neither of these arguments seems entirely cogent to this reader; and, indeed, it would appear that the second is more consonant with the view that the substance in question acts by injuring the tissue and releasing the masked evocator. At high dosages the injury may be sufficient to prevent the tissue from reacting, and an optimum dosage would result. An even more basic issue which has been frequently raised concerns the authenticity of the neural inductions caused by chemical agents. Many biologists would feel on safer

ground if, for example, it could be shown that such induced structures subsequently differentiate into nerve tissue. This question is not answered in the book.

Needed: A Unit of Differentiation

The present status of the organizer problem reveals the embarrassment of a highly experimental science which is unable to express itself in quantitative terms. The need for a unit of differentiation has never been greater. The answer may lie in the direction of the simplification of experiments through the study of isolated parts and processes, as illustrated by the explantation work of Holtfreter and others. Perhaps the ideal measure of differentiation would be in terms of the thermodynamic probability of the developmental state under consideration, the direction of embryonic development presumably being from more probable to less probable arrangements. But such ideals are more easily talked about than realized.

The particular merit of *Biochemistry and Morphogenesis* lies in its encyclopedic completeness. There are many mansions in the embryological house, and Needham is familiar with most of them. The book will be found of great value as a reference work. Although it contains many suggestive ideas, the author, no doubt wisely, makes no attempt at any far-reaching integration of biochemical and morphogenetic data. As is to be expected in a work of this size, there is a certain unevenness in the treatment of various aspects of the subject. In some places, as in that dealing with the chemistry of the organizer, the author has written the best critical accounts to date; in others there is sometimes a tendency to accept or to reject findings on grounds that appear, to this reviewer, to be insufficient.

For those readers who are illiterate in Chinese, your reviewer offers the following translation of the dedication, through the courtesy of Professor S. W. Chair: "This work is dedicated to my friends Misses Li Ta Fei and Lu Kuei Chen. Joseph Li (Needham)."

N. H. Horowitz
Stanford University

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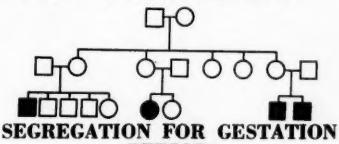
HEREDITY AND LENGTH OF GESTATION

IT has generally been assumed that the length of gestation depends upon the constitution of the individual carrying the fetus.[1] Recent data[2] on the comparative lengths of the gestation periods of Aberdeen-Angus and Hereford cows carrying purebred and crossbred calves, however, have given clearcut evidence that the genotype of the fetus, rather than that of the dam is the determining factor. Purebred Hereford calves are carried in gestation 16 days longer than are purebred Aberdeen-Angus calves, whereas crossbred calves are carried for periods intermediate between the averages of the parent breeds.

My attention was recently called to a human family pedigree which suggests that similar variations in gestation periods may occur in man. In this family pedigree which is shown below, it will be noted that three sisters had gestation periods of 10 months for one or more children, and that two of them had gestation periods of 9 months for other children. The data shown here suggest a fruitful field for further investigation.



SEGREGATION FOR GESTATION PERIOD
Figure 7

Pedigree of three sisters whose children varied in the length of their gestation periods. Solid black indicates children with 10 months' gestations.

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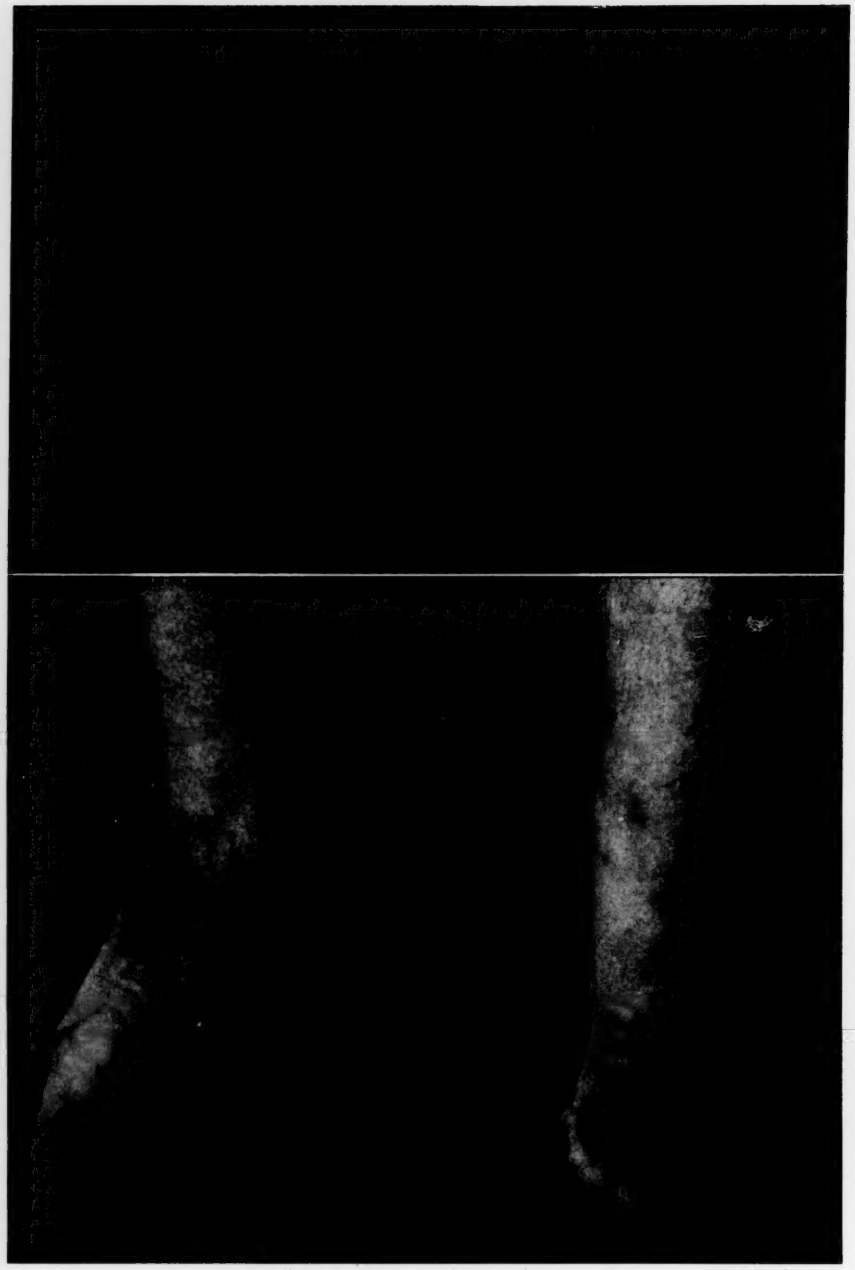


RIGHT HAND AND FEET OF V-16

Figure 8

These photographs show that in this individual there is a greater reduction in the digits of the feet than of the hands. This is the reverse of a trend noted in some other pedigrees for the hands to be more drastically affected.

HEREDITARY MALFORMATIONS OF THE HANDS AND FEET*

KARL A. STILES AND IRENE SCHENKEN PICKARD

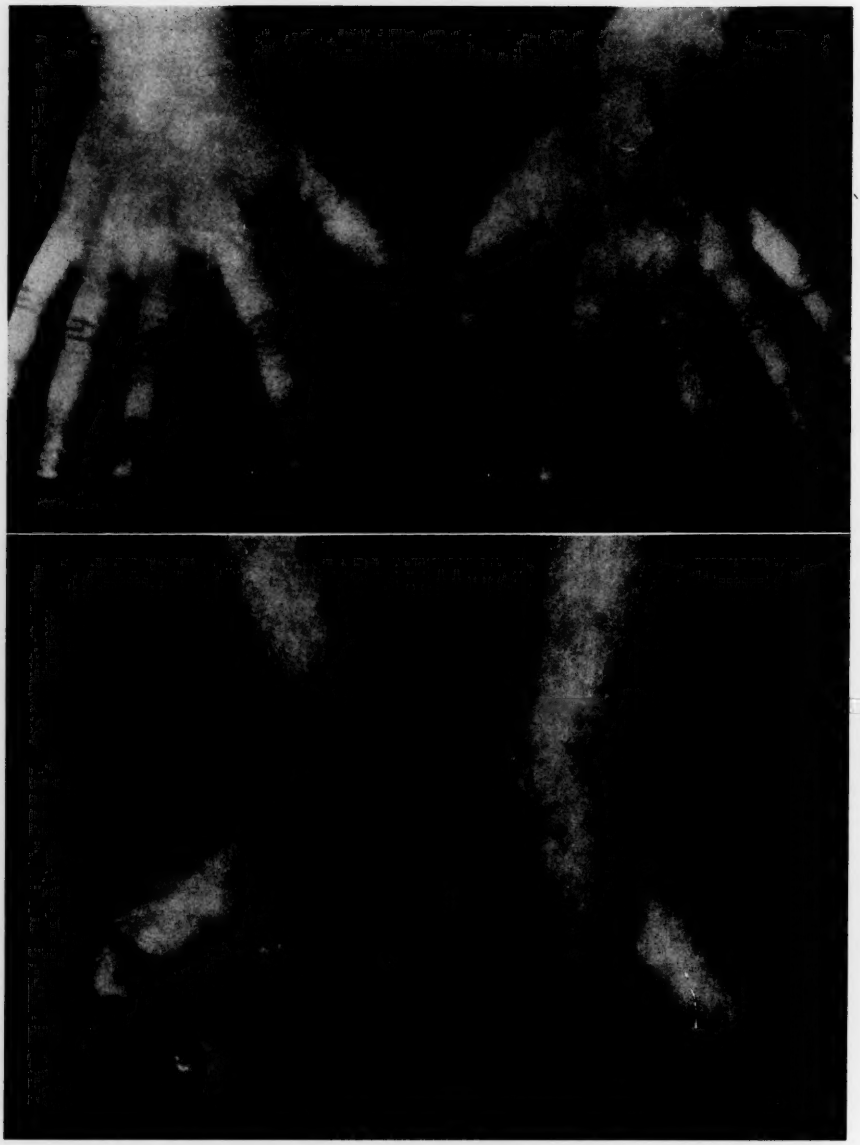
CONGENITAL malformations of the human body have received the attention of anatomists and geneticists over a long period, and within recent years numerous papers on the inheritance of various abnormalities have appeared. The following study should throw further light on this interesting problem.

The hereditary deformities of the family studied by the authors cannot be classified under any one term for they have a wide range, including hands with long thumbs, no thumbs, no finger nails, cleft finger nails, small finger nails, webbed fingers, and missing fingers. Although the feet are not quite as variable as the hands, yet the degree of defect in them is in many cases extreme, as they often exhibit the condition known as "lobster-claw" or split-foot. It is not uncommon for hereditary anatomical anomalies to exhibit considerable variation as shown by Stiles and Weber,[7] and Stiles.[8] Stiles and Douglas[6] have reviewed much of the literature on congenital abnormalities and while some students of the subject would minimize the importance of heredity in the etiology of such defects, nevertheless, most consider it the chief factor.

This case of hereditary malformations of the hands and feet has been traced through four generations (Figure 10). The pedigree chart would suggest that the mutation first came to expression in III-5. The brothers and sisters of I-1-2-3-4 are not known to show the trait. Furthermore, the brothers and sisters of II-1 and II-2 did not exhibit the trait. III-5 has three fingers on one hand and two toes on each foot. IV-1 has a double nail on one finger, and one foot possesses only two toes. IV-4 has long thumbs which turn outward and two of her nails are abnormal. There are only two toes on each of her feet, which makes walking somewhat difficult. V-1 has three webbed fingers with short thumbs and the left hand is small. He has two toes on each foot. V-3 has long thumbs. V-7 has short thumbs on both hands and three toes on each foot. V-9 has three fingers on her left hand and two toes on each foot. V-14 has hands without thumbs and two toes on each foot. The left hand of V-16 is normal except that the thumb is long and two of the nails are abnormal; the right hand is distinctly claw-like as shown in Figure 8. She has two toes on each foot, also shown in Figure 8. VI-3 has long thumbs and there is no information about the feet. VI-7 has long thumbs. Although VI-11 has been designated in the chart as malformed, actually little is known about this person except that IV-4 stated that she had heard that VI-11 was "badly deformed." VI-25 has no nails on his thumbs and only two toes on one foot and three toes on the other. VI-26 has no thumbs, and only two toes on each foot.

Fortunately a medical report on VI-28 was available which makes possible a detailed description of him. He was born with a mesial displacement of the distal phalanges of both thumbs (Figure 9). An effort was made early in infancy to straighten the thumbs with splints but without any apparent benefit. The feet were much more deformed than the hands as indicated by Figure 9. Both feet showed the presence of only the first and fifth digit which are mesially displaced giving the feet a "crab-claw" appearance. According to the mother, displacement of the toes in-

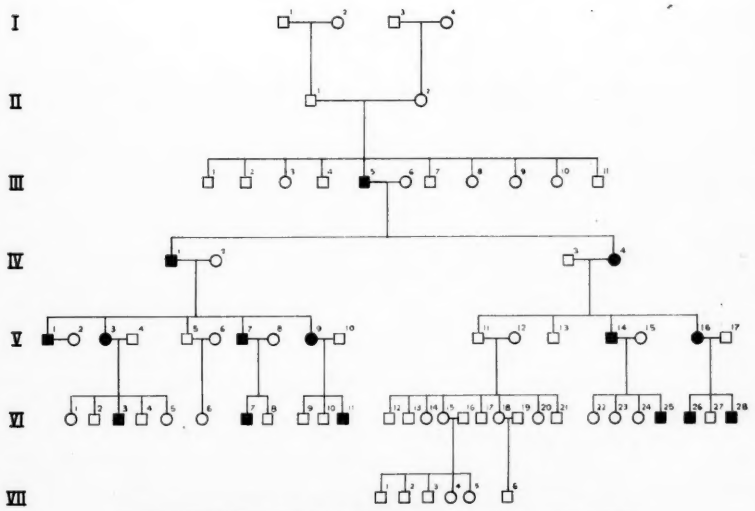
*Contributions from the Science Laboratories of Coe College No. 14 N.S. Aided by an academy grant from the American Association for the Advancement of Science through the Iowa Academy of Science.



"CRAB CLAW" FEET AND DISPLACED THUMBS

Figure 9

Photographs of the hands and feet of VI-28. Here the only defect of the hands is a bend in the thumbs which cannot be straightened out. The feet are much more drastically affected.



INHERITANCE OF MALFORMED HANDS AND FEET

Figure 10

Pedigree of a family showing defect of extremities ranging from gross splitting of the hand or the foot to slight abnormalities of the digits. The intensity of expression of the defect varies unpredictably.

creased somewhat after he started walking. One might expect that great difficulty in walking would be experienced by one with such marked deformity of the feet. However, the medical history stated that the chief difficulties experienced by the patient as a result of these malformed feet were some swelling and tiring of the feet after excessive play, and corns and callouses on the soles of the feet. Naturally, the fitting of shoes was a special problem.

By an operation the congenital deformity of the right foot was corrected by an osteotomy of the great toe, and a plastic repair of the cleft between the great toe and the little toe. On a later date a similar operation was performed on the left foot and both thumbs were corrected by removal of accessory bones in the metacarpo-phalangeal articulation. Then a plaster cast was applied to the left foot holding it in correct position and small mitten casts were applied to both thumbs to promote healing in the correct position.

When he returned to the hospital for a check-up examination, the skin wounds had healed well except for one small area on the right foot. After a later check-up examination, the attending physician stated that VI-28 experienced no pain in walking, there was no difficulty in fitting him with shoes, and all pressure symptoms had disappeared.

School records would indicate that VI-28 was a child of normal mentality. His grades were mostly "A's" and "B's", although there were some "D's" in art and physical education. His generally good school record has been maintained despite repeated absences.

Sociological Aspects of the Case

Although many individuals of this family are considerably handicapped by deformed hands and feet, there is little evidence that affected persons avoided either marriage or parenthood. Perhaps this is due in part to the fact that the family did not really understand that the defect was hereditary. Though IV-4 felt that the character was "in the family," she had difficulty in explaining her

attitude, especially to her sister-in-law who was sure the children had been "marked" during pregnancy. One of the wives thought her having seen a snake caused her child to be "marked." Another member of the family thought that the "marking" was the result of a mother's suffering grief or sadness during pregnancy. Despite the superstitious explanations offered for the appearance of malformed extremities in the family, the wives of affected families were very apprehensive when they became pregnant and one of the women threatened suicide during each pregnancy.

Discussion

As in the case reported by Wightman[9] on syndactyly, this character does not seem correlated with low mentality, alcoholism or inbreeding. As a matter of fact, the affected persons appear not only healthy and normal but attractive except in respect to the specific skeletal defect under consideration.

All members of the family interviewed agreed that the deformity appeared for the first time in III-5. IV-4 remembers a family reunion as a girl at which time her grandparents and great grandparents were present. A discussion arose then regarding the affliction and the only persons whom anyone in the family could remember as having suffered malformations of the extremities were the girl (IV-4), her brother, and her father.

Similar reports of abnormalities of hands and feet including symphalangism, syndactylism, and polydactyly by Wightman,[9] Bailey,[1] Hefner,[4] Standskov,[5] Hedgekotti,[3] and Stiles and Weber[7] seem to agree that many anatomical anomalies may be inherited as single dominant traits. As has been reported by Cockanye,[2] Hedgekotti,[3] and Stiles,[8] the character is not confined to one sex. More males than females are affected, but there appears no good evidence for considering it a sex-linked, sex-influenced, or sex-limited trait.

In this pedigree the distribution and ratio of the affected and unaffected individuals is in complete harmony with a single gene interpretation, in which this particular type of character is assumed to be completely dominant to the normal condition. The cause of the variability of the phenotypes produced by the gene is an open question. The three most common explanations for variations in physical traits are as follows: first, irregularity in the expression of a character is due to an unstable gene; second, environmental factors influencing development are responsible for modifications of the phenotypes; and third, important modifying genes account for the variations in the expression of a trait. The last interpretation appears to be the one preferred by geneticists at the present time, and probably deservedly so; however, environmental factors may contribute to the variability. The hypothesis of an unstable gene seems highly improbable.

Summary

1. This study traces malformations of the hands and feet through four generations.

2. An inspection of the pedigree reveals that the trait may be inherited as a single dominant.

3. Modifying genes, environmental factors, or a combination of both may be responsible for the extreme polymorphism of the character.

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A FOUR-LEGGED RING-NECK PHEASANT CHICK

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EMBRYOLOGICAL monstrosities are of scientific interest in proportion as they throw light upon developmental potencies in various animals or upon the later stages of early reduplications. A four-legged pheasant chick was brought to us in October, 1941, by Dr. R. P. Hunter, Superintendent of Fisheries and Game for the State of Connecticut. It was of the ring-neck variety, and had been hatched in the preceding spring on the farm of Norman Kibbe, Somers, Connecticut, from eggs furnished by the State. Its brain had been removed for some reason and it was in strong formalin into which it had been placed after death at three or four days after hatching. The body cavity had not been opened for good fixation.

This specimen is of particular interest because it illustrates anatomical relations in nearly complete reduplication of the pelvic girdle and attached limb-skeleton, with a single vertebral column not bifurcate posteriorly. The anterior girdle and limbs are almost normally and symmetrically placed in relation to the vertebral column. The posterior set of girdle and limbs are asymmetrically placed to the left of the vertebral column. This was correlated with incomplete neural arches of the vertebrae in the posterior sacral and anterior caudal regions, the centra of all but three of which were complete but asymmetrical in shape. Spina bifida in this region is suspected but has not been verified certainly.

Observations

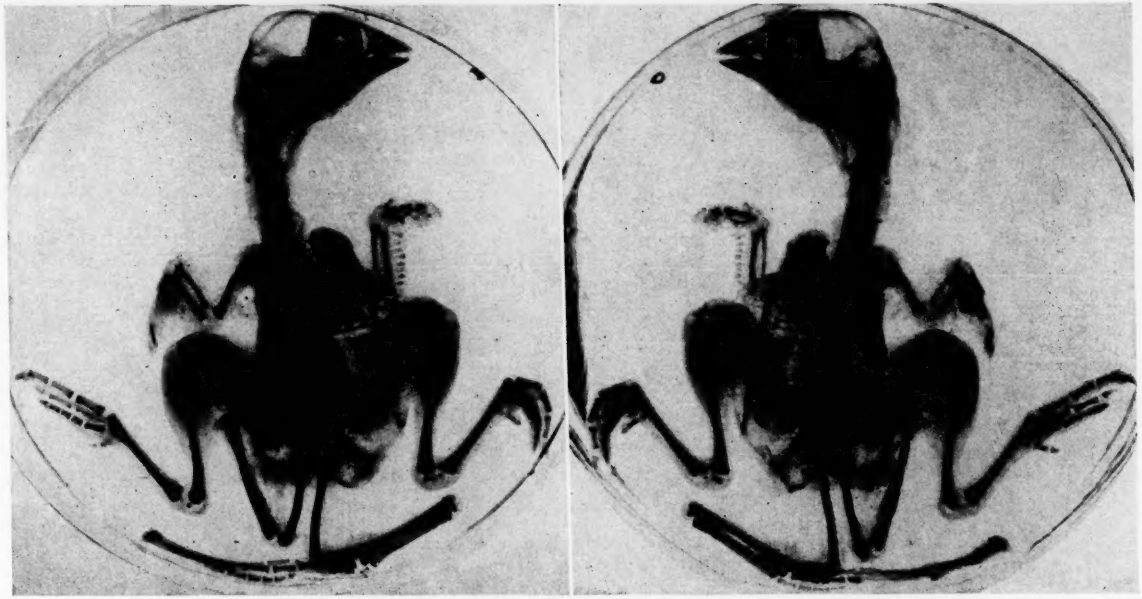
The yolk sac had been drawn into the abdomen but was not absorbed. The usual down of a pheasant chick of its age was present. The two wings were normal in size, position and stage of feather-growth. Of the four legs, one pair was normal in size, position and musculature, so far as could be ascertained by gross dissection and observation. The members of the other pair possessed bones slightly smaller than the first pair and the knee joints faced posteriorly instead of anteriorly. The thighs extended posteriorly, the tibio-tarsus anteriorly and laterally, the tarso-metatarsus postero-medially, with the phalanges continuing in this direction. The position of these secondary limbs indicated that probably they had been swung posteriorly toward the body axis instead of anteriorly as the primary limbs had been, so that pre-axial borders became lateral and post-axial ones became medial in position.

Course of development within the egg shell may have caused this. No nerves were found, although they may have been present, but too small to attract attention, since they were not especially looked for. As might be expected in such a situation, the muscles were all atrophied or had not developed.† These limbs, therefore, consisted almost entirely of the usual long bones of slightly reduced size and nearly normal shape, covered by skin and down. Scales covered the usual segments of the limbs. These legs appeared to emerge at the crest of the back just posterior to the ilium of the primary left leg. This ilium was slightly shorter than that of the opposite side. The tail was bent toward the right in such a way that the supernumerary girdle and limbs extended posteriorly, bending only slightly to the left of the bird's axis of symmetry. In gross dissection it was not apparent whether or not there was a supernumerary pelvic girdle.

The bird was skinned, drawn, and subjected to the Potassium-hydroxide-alizarin-red-glycerine technique for clearing and staining skeletal elements. These and their relations were brought out clearly enough to be photographed with reflected light in front of a brightly lighted white background (Figure 11). The reduplicated pelvic regions with the articulating ends of the femora in relation to the sacral and caudal regions of the vertebral column were photographed again from ventral and dorsal aspects at higher magnification (Figure 12). The shank and foot bones of the left accessory limb were separated from the rest of the limb at the knee and appear in the photographs detached from the rest of the skeleton (Figures 11 and 12).

In the cleared specimen, it is seen that the neural arches of the vertebrae at the level of

*Aided by a grant from the American Academy of Arts and Sciences, 1942.
†See HAMBURGER, V., and M. WAUGH. The skeleton. *Physiol. Zool.* (13)4:367-382. 1940.



FOUR-LEGGED PHEASANT CHICKS

Figure 11

Views of lower side (left) and upper side (right) of four-legged pheasant chick photographed by transmitted light after being cleared.

the posterior two-thirds of the ilia of the primary girdle are incomplete and open dorsally, while the centra are completely formed, except in three or four at the bend of the tail, which are incomplete in the median line. The openings in the neural arches are widest in the region where the ilia bend laterally from the midline, and become narrow slits in vertebrae posterior to this region almost to the last few caudal ones. The caudal bones are displaced toward the right, making the tail assume an angle of about 20° with the median axis of the body. At the region of this bend, the left sides of the incomplete arches are considerably thicker or broader from anterior to posterior face and the accompanying sacral or caudal ribs are longer and broader (Figure 12*A*). On the ventral sides of these same vertebrae the centra are correspondingly broader at the left and taper to the right (Figure 12*B*). This permits the bend of the tail to the right with its vertebrae fitting together snugly.

In the primary pelvic girdle, the ilium of the left side is about 35/39 as long as the right, about 6/7 as wide at the posterior end, thinner, and less densely ossified. The femora of the primary limbs are alike in length and stoutness, as are the rest of the leg bones. The right ischium appears to be slightly longer and slimmer than the left; the left pubis slightly stouter and longer than the right. Ossification into a synsacrum is far from complete at this stage.

The long bones of the supernumerary limbs are shorter, thinner, less robust, and less densely ossified than those of the primary ones. They bear no evidence of muscles. The small ossified centers found in the joints between tibio-tarsus and tarso-metatarsus are not present as they are in the more normal primary limbs. The femora are unequal in length, 21/26 as long and 2/3 as thick at the proximal ends as the primary femora, and much less densely stained with the alizarin-red. This indicates less active ossification, especially at the ends of their shafts. The tibio-tarsus is about 30/35 as long, on the left side, and 32/37 on the right, as the corresponding bones of the primary limbs. The less depth of staining with the dye carries through all the limb bones except perhaps in the phalanges where it appears to be more nearly equal. It seems, therefore, that even the bones of these supernumerary limbs grew and differentiated more slowly than those of the primary limbs with their more normal position, connections, nerves and blood supply. Nerve and blood supply in the supernumerary legs were not studied because of long immersion in the preservative and the smallness and shrunken condition of the specimen.

The accessory pelvic girdle is unique in many respects. No vestiges of vertebral column appear between the two small ilia, broad at the front and tapering to unite in a point posteriorly, bending toward the left, then to the right, and lying above the proximal end of the left secondary femur. Each is about 7/25 as long as the shorter left primary ilium and about the same width at the anterior end. The absence of vertebrae apparently permits the ilia to coalesce at their posterior ends. This suggests that perhaps the intervention of the vertebral column prevents this in the normal girdle. Ischia and pubic bones are present in relation to these ilia and apparently equally well developed on the two sides. The distal

DETAIL OF VERTEBRAE

Figure 12

end of the left pubis was snipped off in removing some of the tissues around it to expose the bones better for photographing, otherwise it would be as long as the right (Figure 12). The ischia and pubes of the two girdles are much more nearly equal in size and shape than are their ilia.

The presence of this more or less complete and symmetrical accessory girdle, without corresponding sacral and caudal vertebrae, indicates either that girdle-development is not dependent upon such bones in normal position relative to it, or that the nearness of the primary set of vertebrae is enough to assure the development of a girdle. This is perhaps a case of double assurance in the sense of Spemann. The conditions found here do not permit a decision on this point.

The position and torsion of the limbs was doubtless largely determined by their position in the shell during development and crowding of the accessory legs may have reduced their nutritive supply and freedom for movement, even if nerve supply was developed. If so, dwarfing of the bones was comparatively slight, except of the ilia. The rudimentary or atrophic condition of the muscles may have been due to one or more of the following factors:—nutritional disturbance by faulty blood supply; failure of trophic effect of nerve supply, either lacking or very rudimentary*; or to lack of space for movement if sufficiently innervated. The reduced size of the supernumerary ilia is in accord with Hamburger and Waugh's findings, as are the smaller reduction of ischia and pubes. These limbs, as wholes, however, are nearer normal size than were their transplants. Joints in these supernumerary limbs appear to be more normally formed than those in their transplants and lacked little more than the small centers of ossification in the intra-tarsal joint. Unlike their transplants, all the phalanges are present in these legs. This anomaly differs in these respects from what might be expected to result from accidental transplantation of some tissue from the posterior limb-field during embryonic life, if the results of Hamburger and Waugh are of wide application.

Summary

The anatomical relations of the caudal and sacral vertebrae, primary and supernumerary pelvic girdles and legs, of a four-legged ring-neck pheasant chick, three to four days after hatching, are described and shown in photographs.

The condition appears to represent the result of accidental transplant of limb-field material or separation of it into two parts in series along the axis of symmetry rather than a posterior bifurication or twinning of the embryo.

*See Hamburger and Waugh, *ibid.*

Individual Differences in Human Blood

Recent reports in the JOURNAL have described how the large number of antigens in cattle blood make it possible to tell the blood of any one animal from that of any other animal. Studies of the inherited antigen differences in pigeon blood tell substantially the same story. Writing in the *Journal of Immunology* (Feb. 1943) the same University of Wisconsin team whose researches have individualized the blood of cattle and pigeons now find that by appropriate techniques it may be demonstrated that "human serum contains antigenic components by which the serum of an individual can be distinguished from that of others." In other words, underlying the larger categories such as the blood groups, the M-N alleles and the Rh series are still finer differences which can be revealed by appropriate immunological fractionation.

The method of demonstrating these differences is to inject human blood from a test individual into a rabbit. The rabbit makes antibodies against this specific blood. By differential absorption it is shown that specific antibodies peculiar to this particular individual remain in the rabbit serum after all the other known factors are eliminated.

As yet the evidence does not show whether the differences are greater or are due to "metabolic products or to allergens in the sera of various persons." Investigations are under way to test this point.

SOME ANOMALIES IN PIGS*

E. J. Warwick, A. B. Chapman and Burr Ross

SEVERAL abnormalities have been noted within the past two years in three different herds of swine with which the authors have some association. They are being reported to supplement the evidence already available from other studies on the hereditary bases of these or similar abnormalities, and to furnish further data on their occurrence in different breeds.

The congenital abnormality noted in Herd I (Duroc breed) is characterized by hydrocephaly and rudimentary tail. Those noted in Herd II (Chester White) included atresia ani, hernia, hair whorls, front and hind leg deformity, cryptorchidism, kinky and short tail and a tendency to circle to the right. Herd III (Poland China) yielded a hydrocephalic pig, a cryptorchid and another with a frontal fissure and cleft palate.

The available information on these anomalies does not constitute sufficient evidence for any dogmatic assertions as to their genic bases, but heritability of most of the variants is indicated.

Herd I

The birth of a number of abnormal pigs in a Duroc herd was called to the attention of one of the authors (E.J.W.) in 1941. One of the defective pigs, a typical specimen, was available for close examination (Figure 13*A*). It was characterized by a pronounced hydrocephalic condition and a rudimentary tail. Many of the abnormal pigs were born alive, but lacked nervous coordination and soon died.

All of the defectives were sired by one boar. Before the condition had been identified, several of the sows had been remated to him for second litters. Thus, the data for two farrowing seasons are available. That for the spring farrow is based on the memory (six months later) of the owner, and in the litters where the information is believed to be fairly accurate, at least ten of 39 pigs were defective. Some of the defective pigs are known to have been born in other litters, but the owner could not recall how many. The data for the fall farrow are accurate and complete, and show that 12 of 61 pigs farrowed in six litters were defective. Several of the sows which produced defective pigs when mated to the above boar, were mated to other boars previously or subsequently with no abnormal pigs resulting from the matings.

All sows in the herd traced to a single foundation sow farrowed in 1929 and several boars have been bred to her and her descendants during the intervening years. The pedigrees of the individual sows have not been kept since 1936, but pure breeding has been practiced, and with one exception the extended pedigrees of all the foundation animals were available for study. The mates of the sire of the defective pigs were closely related to each other, but not to the sire. So far as the pedigrees show they were not inbred. The missing pedigree is that of the boar used the year previous to the outbreak. He was the sire of several of the sows, but probably did not carry a gene for this condition since he sired two normal litters when bred to a sow who later produced defective pigs.

The preceding facts indicate that the occurrence of this lethal condition can be explained on the basis of a single recessive gene. What is probably the same condition was described by Blunn and Hughes[2] in a Duroc herd in California, and was also interpreted as a simple recessive. Many of the pigs they described had light colored hair, and while those reported here were not noticeably lighter in color than other pigs in the same

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herd, most of the animals in the herd are lighter than the average of the breed. Professor Hughes kindly furnished a three generation pedigree of the boar apparently responsible for introducing the gene into their herd. No animals in any of the four generation pedigrees of the herd reported here also appeared in it. If the undesirable genes in the two herds are the same and came from a common source, this must have occurred several generations ago.

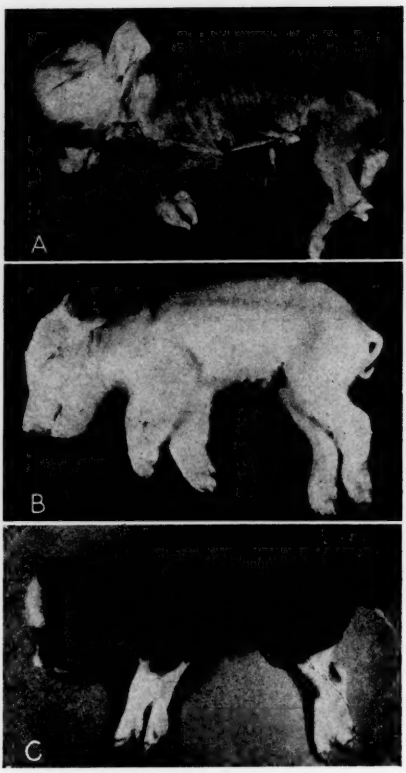
The frequency of this undesirable recessive gene in a single herd is remarkably high, since its presence was demonstrated in at least seven or eight of nine related but non-inbred sows. This incidence should not be considered representative, however, as it may well be that it was the unusual number of defective pigs which attracted attention in the first place.

If, as seems likely, the same gene is involved in the two outcrops of this condition, its presence in two areas as widely separated as the Middle West and California indicates that the gene has been considerably scattered through the Duroc breed. Additional weight is lent to this suggestion by the herd records which indicate that two separate introductions were made of the gene into the herd reported.

Herd II

The leg deformity of the Chester Whites (Figure 13*B*) is strikingly similar in appearance to the case reported in German Landrace by Walther, Prűfer and Carstens,[13] Carstens, Wenzler and Dűrr[3] and reproduced in this JOURNAL by Berge.[1] The front legs are stiff and the feet are drawn slightly in the postero-dorsal direction. The hind feet seem to be similarly affected, but thickening of the hind legs is not evident. The forelegs owe their thickening primarily to the presence of a large amount of gelatinous material in the connective tissue surrounding the bone. The bones themselves were indistinguishable from those of a normal pig.

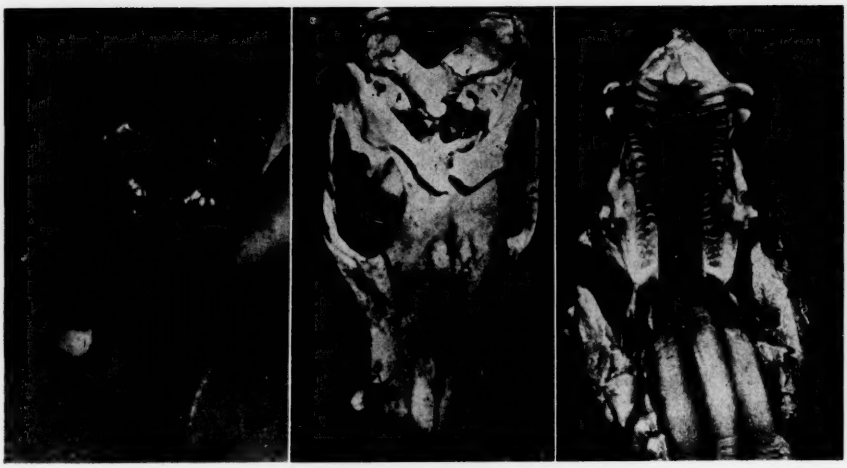
There were 71 litters produced in Herd II during a two year period; and 43 of these litters traced back to a single boar (sire *A*) in the second to fourth generation. All the abnormalities in this herd noted here were found in nine of these 43 litters. Twenty-eight other litters showing no more than remote relationship to sire *A* gave no abnormal individuals in three farrowing seasons. Furthermore, all four of the cases of leg deformities, both of the atresia ani cases, seven of the nine cases of hair whorls, three of the five cases of kinky tail, and two of the four hernia cases resulted



THREE LITTLE PIGS

Figure 13

Pigs showing various defects as follows: *A*—Duroc-Jersey pig suffering from hydrocephaly and with a short tail. *B*—A Chester White pig with thick forelegs. *C*—A Poland China hydrocephalic pig.



POLAND CHINA DEFECTS

Figure 14

The Poland China pig shown in detail here occurred in the same herd as the hydrocephalic pig shown in Figure 13*C*. This individual had a defective skull so that the brain was exposed as well as a cleft palate. Details of the skull and of the palatal defect are shown in the center and right hand photographs.

from mating a single boar (sire *B*) to four of his ½-grandnieces, his sire, boar *A*, being their paternal great-grandsire (the inbreeding of the pigs is about three per cent). Matings of sire *B* to three other ½-grandnieces (23 pigs farrowed), however, yielded no abnormal pigs.

The analysis of their own limited data and results of Kinzelbach[7] and others led Carstens et al[3] to postulate a single recessive with complete "penetrance" in the homozygote as the basis for "Dickbeinigkeit" (thick legs) and another single recessive with reduced penetrance (73%) in the homozygote for "Afterlosigkeit" (atresia ani). They also suggest that there is linkage between atresia ani and thick legs. If we consider only those litters in which at least one pig with atresia ani or stiff legs appears and assume that the parents are heterozygous, then the expectation of the character appearing if penetrance were complete would be greater than 25 per cent, because some matings of heterozygotes may not, on the basis of chance, produce recessive individuals. Actually in these selected litters in our data there were only two pigs with atresia ani out of 23 pigs in two litters and four pigs with deformed legs out of 36 in three litters. Obviously, these percentages are markedly less than the expectation noted above.

With regard to these two characters being linked, our observations are consistent with Carstens et al.[3] in the sense that both characters have occurred in stock with similar ancestry. Also, out of the five pigs showing either atresia ani or deformed legs, one showed only the former, three only the latter and one both of these characters. This, too, is consistent with the idea of linkage. Little can be said from our data regarding the genetic basis for the abnormalities other than atresia ani and deformed legs. So far as they go they do not appear to be inconsistent with the interpretation of Craft and Warner[4] and Nordby[10] on whorls, Warwick[14] or Berge[1] on hernia, and Nordby[11] on kinky tail.

A genetic basis for these characteristics is indicated by the higher frequency of all these abnormalities in the more highly related and inbred pigs. Further-

more other sows in the same herd and managed essentially in the same way, farrowed only normal pigs during the two seasons in which these abnormalities were observed.

The exact mode of inheritance of each is not discernible from our data, nor is it possible to decide whether pleiotropism or linkage combined with variable genetic expression is responsible for what do not appear to be accidents of development.

Herd III

The occurrences in a Poland China herd of an isolated case of a hydrocephalic pig (Figure 13*C*) and of another pig with a naked brain extrusion and cleft palate (Figure 14) provide no basis for a decision as to the mode of origin of these defects, except to suggest "embryological accident" as the descriptive term.

The pig with brain extrusion and cleft palate appeared in a litter with seven normal pigs. The brain protruded through a frontal fissure in the median line 40 mm. wide and extended from between the posterior angle of the eyes to a point about 40 mm. postero-dorsally. The cleft in the palate was complete and more extensive than those illustrated by McPhee et al.[8] in this JOURNAL.

The bones of the skull of this pig show marked irregularities as compared to those of a normal new-born pig (Figure 14). The most apparent of these are the great reduction in size of the parietals, the absence of the supra-occipital and the very slight development of the lateral palatine processes of the maxillaries.

The hydrocephalic Poland China (Figure 13*C*) was quite similar in appearance to the Duroc case reported above, with the exception that a tail of normal length was present. This pig occurred in a litter of eight pigs and was the only one showing any abnormality.

Summary

A variety of abnormalities (hydrocephaly and rudimentary tail in one herd; atresia ani, hernia, hair whorls, front and hind leg deformity, cryptorchidism, kinky and short tail, and tendency to circle to the right in another; and hydrocephaly, cryptorchidism, and frontal fissure and cleft palate in a third) have been noted by the authors in three herds representing three different breeds of swine during the past two years. A genetic basis for, and a genetic association between some of them is indicated from their history. The exact nature of inheritance is not established for any but is strongly indicated in the case of hydrocephaly (simple recessive) in Durocs.

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